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EMBRYOLOGY.[1]

Development of an Isopod—The first paper of M. Louis Roule on the development of the Crustacea has just appeared.[2] He has studied, as a representative of the Edriopthalmia, the Isopod, *Porcellio scaber*, Leach, with especial attention to the first stages of development. The origin of the blastoderm, of the germ layers, and of the rudiments of the organs, are considered in great detail, and there is, besides, much general discussion on the significance of these processes among Arthropods. This first paper will be followed by three others; one on the Decapods, one on the Copepods and Branchiopods, and a third on general questions.

Though Bobretzky, in 1874, established the chief features of the development of Isopods from a study of *Oniscus murarius*, a detailed examination of the development of the group was much needed; and M. Roule has also wished to throw more light on the question of relationship between Annelids and Arthropods. He has been led to believe that the early stages of the Crustacea do aid us materially in testing such an affinity.

The eggs of *Porcellio scaber* develop in the brood chamber of the mother, the early stages (including segmentation, the formation of the blastoderm, and establishment of the germ layers) requiring a proportionately long time, about two weeks, while the rest of embryonic development takes but three weeks.

The unsegmented ovum is mainly a mass of nutritive yolk, with the greater part of the formative material on the surface in the form of "*islands*" of protoplasm. The food yolk consists of a great number of large vitelline granules in a protoplasmic groundwork. Toward the periphery the granules are smaller, and the islands of formative yolk, though finely granular, are mostly formed of the protoplasmic groundwork. In a surface view one of the islands of protoplasm is found constantly at the anterior pole, and is seen to be larger than the others. This is the germinal disc, and it contains the only nucleus in the ovum. The other islands have no constant position or size; they are continuous with the central deutoplasm (as is also the germinal disc),

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[1] Edited by E. A. Andrews, Baltimore, Md., to whom abstracts, reviews and preliminary notes may be sent.

[2] Annales des Sciences Naturelles, Vol. xviii, Nos. 1, 2, 3 (sér. 7), with 10 plates.

and separated from one another on the surface by deutoplasm. The nucleus in the germinal disc divides, and its descendants scattering in the protoplasm form a syncitium adherent to the surface of the food yolk. As the disc spreads, the central protoplasm divides up into cells around its nuclei, while the periphery remains a syncitium. This syncitium is soon broken up into cells, and as the blastoderm thus formed extends, it annexes more formative material as it reaches the islands of protoplasm. The periphery of the blastoderm is thus continually added to, and the protoplasm forming the growing edge is constantly supplied with nuclei from the centre of the disc, around which in their turn new cells are formed. Besides the protoplasm added from the islands, formative material is also supplied from the centre of the ovum among the deutoplasm. In this way the blastoderm gradually extends over the egg from the anterior pole ventrally and laterally, until it finally closes in at the posterior pole near the dorsal surface. (This type of segmentation seems to fall between Korschelt and Heider's III b. and IV.) Soon after the first cells of the blastoderm have become well defined at the anterior pole, they begin to split off an under layer, the mesentoderm (Roule's protendoderm). This layer is steadily added to as the blastoderm spreads, by a repetition of this process of splitting tangentially, by incorporating new cells thus formed at the anterior edge of the blastoderm, and by a division of its own cells. The anterior pole of the egg is the growing point of the mesentoderm. The cells lie for the most part along either side of the ventral mid-line, in two ridges projecting into the yolk, in the anterior region of the embryo. The cells being amoeboid, however, wander dorsally and posteriorly, where they lie as elsewhere in the outer portions of the deutoplasm. By this time the cells of the ectoderm have flattened, except in two regions, into a single layer. At one place where the brain is to appear, a rapid division of nuclei and fusion of cells takes place, until a syncitium is formed projecting into the yolk. A similar syncitial mass is formed on the ventral mid-line, to be the ventral cord. These two areas are connected by ectoderm, which will later be the œsophageal ring. Nineteen pairs of appendages gradually appear from before backward. At first they are formed of an ectodermic sheath with a core of nutritive yolk and scattered mesentoderm cells; but soon the nutritive yolk is absorbed, leaving merely the mesoderm cells within. While the nervous system is becoming more distinct, and the appendages are growing and increasing in numbers, a proctodeal invagination, which appeared at the point where the blastodermic disc closed in, and a stomodeal invagination, which appeared at the anterior pole, both grow into the yolk mass towards the centre of the egg. The proctodeum is a narrow, straight tube, which finally reaches the anterior portion of the body and comes into contact with the stomodeum. The latter begins in a short, straight œsophageal portion at the base of the mandibles, which is distended at its central end into a vesicle resting against the blind end of the proctodeum.

The most striking changes during this period are, however, found in the mesentoderm. It becomes differentiated into two layers, mesoderm and endoderm. The mesentoderm (or protendoderm) has, as has been seen, collected especially in the anterior end of the body, on either side of the median line. In the rest of the body it formed a layer of scattered cells in the surface of the yolk under the ectoderm. The lateral anterior masses become slowly marked off into a dorsal and a ventral portion. The dorsal portion forms a plate of cells on either side of the median plane in the anterior region of the body. The ventral part forms two ridges of cells (one on either side of the ventral mid-line), which are numerous, closely packed, and run down into the appendages. At the base of each pair of appendages there is a collection of these cells, to become muscles of the limbs. This gives the mesodermic ridges a metameric appearance. The two lateral dorsal plates become more and more clearly defined and enlarged. They are concave toward the yolk mass enclosed between them, and as they grow and meet on the mid-line, they unite. In this way a mass of yolk in the centre of the embryo is gradually included in a layer of cells, endoderm, originating from the mesentoderm. Since, however, the union of the endodermic plates is gradual, and since they meet first anteriorly and ventrally, the enteric vesicle formed by them is open behind and above for some time. The endoderm is now distinctly marked off from the rest of the mesentoderm, and has arisen from anterior lateral collections of this layer and from its dorsal portion. The rest of the mesentoderm becomes mesenchymatous mesoderm. It is found everywhere beneath the ectoderm, especially ventrally. One other thing is more and more evident in this region, where the mesoderm is collected most: the yolk has been absorbed gradually, and the mesenchymatous elements are here bathed in plasma. This absorption of yolk will continue rapidly from now on, proceeding from the ventral toward the dorsal surface of the embryo.

During the last period of development profound changes take place, ending in the fully-formed young crustacean ready to leave the egg-membrane. The ectoderm soon secretes a cuticle, while the appendages elongate and become segmented. Those belonging to the head draw together around the mouth, and those in the abdominal region flatten and become pleopods; while the thoracic limbs become the longest appendages of the body, with the exception of the second antennæ. At first there is no external segmentation of the body, but gradually a head region is marked off from the thorax by a groove. Posteriorly, the thorax and abdomen are also pretty clearly marked, the latter being of smaller segments. The grooves between the segments appear first ventrally and grow up towards the dorsal surface. Later dorsal grooves appear and grow down to meet the ventral ones. Finally the abdominal, and the two or three most anterior thoracic segments, are completely marked off by circular grooves. The thorax is the last region to become segmented. Its mid-dorsal portion is raised into a peculiar hump, which is very prominent for a time, but gradually disappears as the development proceeds to a finish.

The proctodeum and stomodeum have gradually approached and met in the thoracic region as described, and finally the point of union breaks through, and the digestive tract is continuous in its whole length. In the first period the enteric vesicle had become almost entirely closed in around a mass of yolk in the centre of the embryo; now it is entirely closed and becomes greatly changed. A deep groove pushes in along its ventral surface from in front backward. It deepens towards the dorsal surface, and finally meets a groove from above. They split the enteric vesicle into two halves which are however united anteriorly by an unsplit portion. This anterior stem, bearing the two enteric lobes behind, (later on the two primary enteric lobes split into two secondary each) lies just at the point where the proctodeum and stomodeum meet, and where their cavities become continuous it opens into the alimentary canal thus formed. As M. Roule says: "Such a disposition is found among all crustacea, with the constant relation of the enteric vesicle with its lobes attached to the digestive canal in the zone of union of the anterior and posterior intestines." "Considering the entire digestive tract then, the whole system, canal and annexes, originates from three rudiments which are at first independent of each other and later joined into a single system. Two of these, the stomodeum and proctodeum, arise from the ectoderm, while the third comes from the entodeum. A like structure and like triple origin is to be found in the other Arthropods, but with an important difference: the proctodeum does not extend so far into the body as that of the Crustacea; its anterior end remains some distance behind the enteric vesicle; it unites with the enteric vesicle at its posterior end, while the stomodeum joins the vesicle at its opposite end. The enteron is thus interposed between the anterior and posterior intestines, becomes a part of the digestive canal and forms the mid-gut, which Crustacea almost completely lack." The endoderm, hence, arises internally from the protendoderm, and not by invagination. There is no gastrula among Arthropods, the apparent gastrula invaginations being really stomodeal invaginations. The alimentary tract arises from three rudiments in an entirely different way from the process followed in animals with true gastrulation. Every little depression on the Arthropod blastoderm, M. Roule says, has been thought to be a gastrula when once the necessity for finding one was thought established by the early workers on the germ layers. However, gastrulation is not so important as the results of it, and M. Roule suggests that a very important difference between Arthropods and other Cœlomates is the fact that their digestive tract is not formed from any of the so-called gastrulas.

(It will be noted that Heymons, in a recent paper, has also given up the idea of endoderm formed from a gastrula invagination, deriving the whole digestive tract in insects from the stomodeum and proctodeum. Korotoneff, too, has adopted Heymons' view to a great extent.)

As development proceeds, the yolk enclosed by the enteric vesicle is gradually absorbed, the brain and ventral cord become differentiated, and the yolk mass in the body cavity is rapidly reduced. This reduction is effected by phagocytes floating in the plasma, which washes the edges of the yolk. They eat it away until it is confined to the dorsal portion of the thorax, where it forms the hump mentioned above. Besides these wandering cells, other cells of the mesoderm elongate become grouped together and form muscle bands crisscrossing through the body cavity. By the end of this period all trace of metamerism has vanished from the mesoderm. The appearance of metamerism, noticed at an early stage, was due to collections of mesoderm cells at the bases of the successive pairs of appendages, before they had pushed out sufficiently to accommodate those cells destined to shove in and form the inner structures of the limbs. The disappearance of this apparent metamerism in later stages is due to the segmental collections of cells having moved into the limbs to their definitive position. "This fact shows undoubtedly how the metameric disposition of the ventral mesoderm is bound up in the distribution of the appendages in regular pairs as cause to effect. The first is the result of the second, and has no other value whatsoever."

In speaking of the external segmentation of the body, M. Roule says:

"The annelidan structure of the organism manifests itself at a later date than the production of the appendages. The folds between the rings pass rigorously between the pairs of appendages. The relation of cause and effect is apparently evident. This structure is, as the temporary metameric disposition of a part of the mesoderm, a result of the presence of limbs on the body and of their distribution in pairs placed regularly one behind the other at equal or almost equal distance apart. The object is to facilitate movements of the body especially flexion, and is of no other importance. The morphological value of this segmentation of the body into a metameric series is hence most plain; it is secondary, and not primitive, in spite of its analogy to annelids and vertebrates, and it is to be associated with the existence and arrangement of the paired appendages."

In another place the difference between the metamarism in the two groups is put as follows: "In the annelids the metameric division of the mesoderm is due to a regular increase of cavities in this layer from one end to the other. The appearance of such spaces is not at all dependent on the presence of appendages, for it precedes their origin and takes place even when they are lacking. Finally these cavities enlarge equally and surround the intestine."

As to the Arthropods: "Only a part of their mesoderm assumes a metameric appearance, the rest remaining mesenchymatous. This segmental arrangement is not at all a result of multiplication of cavities, but the result of a compact grouping of cells due to an inequality in multiplication. The spaces which appear finally in the mesoderm are irregular, numerous, and in no way related to the segmental arrangement. This is dependent on the presence of appendages, since it is established after these are produced and so that a metamere lies above each appendage. The relation is so intimate as to compel the inference of cause and effect. Finally, in no case do the mesodermic cavities enlarge in a regular way to surround the intestine."

Before the embryo is set free, the hump on the back, due to the yet unabsorbed food yolk in the dorsal part of the body cavity, disappears on the complete absorption of this yolk. This hump has been described as a "dorsal organ," but it is easily seen to be no organ at all, merely the last of the food yolk.

M. Roule devotes considerable space to the establishment of his view as to the formation of the germ layers in Arthropods and their homologies with those of other cœlomates. He regards the whole process of the spreading of the disc-shaped blastoderm as a process of planulation. No epibolic gastrula is formed, he claims. The planulation consists in splitting a central layer of cells belonging to the food yolk from a superficial ectoderm. The protentoderm does not arise, according to this, from the ectoderm, but both layers are the result of a division of the blastoderm. Just as in any planula of this sort (lecithal), there is an external epithelial layer of cells, while the internal ones are connected with the yolk.

Other Crustacea show a simpler and more typical planula. Here, after a total segmentation resulting in a collection of pyramidal cells, the central ends containing the yolk divide off, forming an inner layer of cells (protendoderm), while the peripheral remains as the ectoderm. In the Isopods the mesentoderm separates from the yolk mass as amœboid cells. In insects the condition is more complicated, but essentially the same. The cells produced from the formative yolk travel to the periphery and become the blastoderm, which divides as in the Crustacea into the mesentoderm and ectoderm. The cells from the centre, which do not reach the blastoderm before its splitting into two, are really blastoderm cells retarded from becoming ectoderm. They become mesentoderm cells. M. Roule distinguishes them by the term "inner blastoderm."

"By whatever method formed, the resulting planula is composed of a peripheral blastoderm and a central deutoplasm. It is centrolecithal. This planula is peculiar to Arthropods and some Hirudinea."

"The lecithal planula of other animals belong to Cephalopods, some Tunicates, and many vertebrates (Teleosts, Selachians, Sauropsida). Here, too, the central yolk mass is enclosed by a disc gradually spreading over the surface; but in these cases the blastoderm divides into two parts, one thick, situated at the place where the disc started to spread, and alone destined to give rise to the embryo, while the rest is reduced to a thin membrane, limiting the yolk and absorbing it, but not forming any part of the adult. These two portions of the blastoderm are the embryonic zone and the vitelline zone. They are contiguous, and the nutritive mass is not placed in the interior of the young individual. In Arthropods the condition is quite different. The blastoderm is entirely embryonic, and encloses all the deutoplasm which forms an *internal* vitelline vesicle, and not a contiguous one. The centrolecithal condition of the planula and the genetic unity of the blastoderm so constant among Arthropods, lends to these creatures an autonomy separating them from other cœlomates."

The germ layers of Arthropods are not, according to M. Roule, homologous with those of other cœlomates. The ectoderm, however, he believes to be homologous in origin and history in all cases. Homology means to him identity of origin in time and space, and he believes that two systems with like fates, but dissimilar origins, are not homologues.

The protendoderm of Arthropods is a mesenchymatous tissue arising by migration, as in a planula of the hydrozoa. That of other cœlomates is epithelial from the start, and arises by gastrulation. Hence, in origin and character the two are essentially different.

"The investigations of many observers on the development of sponges and hydroids have shown that in the cœlenterates the germ layers may be formed by other processes than gastrulation. To-day it seems to M. Roule impossible to consider the germ layers of the metazoa as homologous. They differ from one another in origin. The protendoderm (mesentoderm) of Arthropods does not correspond to that of other Cœlomates; but among Arthropods it is homologous, and among other cœlomates it is homologous. The difference between the lecithal planula of Arthropods and similar ones of other cœlomates lies in the origin of the endoderm in the latter by a true gastrulation.

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